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Two New Species of Vestimentiferan Tubeworm (Polychaeta: Siboglinidae a.k.a. Pogonophora) from the Brothers Caldera, Kermadec Arc, South Pacific Ocean

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Two new species of vestimentiferan tubeworm collected from the Brothers Caldera in the Kermadec Arc, South Pacific Ocean, are described here, based on morphological and molecular analyses, including sequence comparisons of over 600 bp of the mitochondrial COI gene. *Lamellibrachia juni* sp. nov. differs from congeneric species in having flexible and thin-walled tubes, up to three pairs of lamellar sheaths, and similarly sized cuticular plaques on the vestimentum and trunk. *Oasisia fujikurai* sp. nov. differs from its sole congener in having eight pairs of branchial lamellae instead of up to 20. *Oasisia* and *Ridgeia* are shown likely to constitute a monophylum, but are retained as separate genera for now. The relationships between this clade and the genera *Tevnia* and *Riftia* remain unresolved. Within the monophyletic genus *Lamellibrachia*, *L. juni* sp. nov. is closest to *L. sp. L7* from the Manus Basin.

Key Words: Brothers Caldera, Kermadec Arc, Polychaeta, Vestimentifera, *Lamellibrachia*, *Oasisia*, *Ridgeia*, COI gene sequence, taxonomy, monophyly.

Introduction

More than 30 years of deep-sea research using scientific submersibles have provided a rich supply of vestimentiferan tubeworm material and led to the description of numerous new taxa in this group from the species to the phylum level (Webb 1969; Van der Land and Nørrevang 1975; Jones 1985; Southward *et al.* 2002), but morphological analysis alone may not be ideal for vestimentiferan taxonomy. Confusion in interpreting morphological changes during growth, as well as individual variation, resulted in the description of an invalid species, which was subsequently synonymized with another species of the same genus after observations had been carried out on additional specimens (Jones 1985; Southward *et al.* 1995). The unique ecology and body structures of deep-sea vestimentiferans have stimulated a number of molecular and cladistic analyses leading to numerous phylogenetic cladograms for vestimentiferan tubeworms (Williams *et al.* 1993; McHugh 1997; Black *et al.* 1997; Rouse and Fauchald 1997; Kojima 1998; Halanych *et al.* 1998;

Rouse 2001; Gardiner *et al.* 2001; Kojima *et al.* 2001, 2002, 2003; Hurtado *et al.* 2002; Schulze 2003; McMullin *et al.* 2003; Andersen *et al.* 2004). But molecular data alone may also be insufficient. For example, in the case of the genus *Escarpia*, the COI (cytochrome oxidase *c* subunit I) sequences cannot discriminate the three included nominal species (Anderson *et al.* 2004).

During the YK04-9 SWEEPVENTS Cruise of R/V *Yokosuka* of the Japan Agency for Marine-Earth Science and Technology (JAMSTEC) in 2004, hydrothermal vent fields in the Brothers Caldera in the Kermadec Arc were surveyed using the submersible *Shinkai 6500*. In a single hydrothermal vent field on the north-western wall of the caldera, where acidic (around pH2) and Al-rich hydrothermal fluid was sampled (de Ronde *et al.* 2005), two kinds of vestimentiferan worm were discovered. Larger worms belonging to the genus *Lamellibrachia* thickly colonized a soft substrate in proximity to a hydrothermal vent, while a smaller species of the genus *Oasisia* made dense clumps on a sulfide structure with diffuse flow. Here we use both morphological and molecular analyses to describe these two new species.

Materials and Methods

Vestimentiferan specimens were collected from the Brothers Caldera in the Kermadec Arc at about 1600 m depth. The manipulator arm of DSRV *Shinkai 6500* was used to remove tubeworms from the substratum and place them into an external cage attached to the submersible; they were brought up to the surface without any regulation of pressure. The sampling data are provided in the taxonomic section below. Most of the examined specimens were fixed aboard ship in 10% seawater formalin and preserved in 70% ethyl alcohol, and the rest were preserved in 99% ethyl alcohol without formalin fixation. Nine additional specimens of *Oasisia* were used only for measurement of their tubes, because the badly fixed soft bodies were not suitable for measurements or other observations. Specimen drawings and photographs were made respectively with the aid of a camera lucida (Olympus SZX-DA) and a digital camera system (Nikon Coolpix 950) attached to a dissecting microscope (Olympus SZX12). Additional morphological observations were made with a light microscope (Olympus BH2). The type specimens are deposited in the National Science Museum, Tokyo (NSMT). The polychaete classification proposed by Rouse and Fauchald (1997) is basically followed in this study. In this classification, all pogonophores and vestimentiferan tubeworms are placed in the family Siboglinidae.

Three specimens of each species were taken from the same haul as their type specimens for DNA studies. In the laboratory DNA was extracted from the vestimentum by grinding, digestion with sodium dodecyl sulfate, and extraction with phenol and chloroform. An approximately 700 base-pair (bp) segment of the mitochondrial gene for COI was amplified by the polymerase chain reaction (PCR) with the universal COI primers LCO1490 (5'-GGTCAACAAATCATAAAGA TATTGG-3') and HCO2198 (5'-TAAACTTCAGGGTGACCAAAAAATCA-3') (Folmer *et al.* 1994). PCR conditions were as follows: 94°C for 60 s; then 30 to 40 cycles at 92°C for 40 s, 50°C for 60 s, and 72°C for 90 s. GenereleaserTM (BioVenture Inc., Murfreesboro, TN, USA) was used to sequester products of cell lysis that might have inhibited the polymerase.

The nucleotide sequence of 630 bp of each amplified fragment was determined bidirectionally with an automated sequencer (ABI3100; Applied Biosystems Inc., Foster City, CA, USA) using the same primers as those for PCR.

The genetic distance between sequences was calculated by Kimura's two-parameter method (Kimura 1980). Phylogenetic trees were constructed by the neighbor-joining (NJ) method (Saitoh and Nei 1987) with the program from the MEGA2 package, Version 2.1 (Kumar *et al.* 2001) and the maximum-parsimony (MP) method using the multiple equally parsimonious heuristic search option of PAUP, Version 4.0b10 (Swofford 2002), with tree bisection-reconnection and 1000 random addition sequence replicates.

Taxonomic Account

Family **Siboglinidae** Caullery, 1914

Genus ***Lamellibrachia*** Webb, 1969

Lamellibrachia juni sp. nov.

(Figs 1, 2, Tables 1, 2)

Material examined. Holotype: Brothers Caldera, *Shinkai 6500* Dive 851, 26 October 2004, 34°51.652'S, 179°03.536'E, 1604 m, female, NSMT-Pc 9. Paratypes: same sampling data as holotype, 4 females, 3 males, NSMT-Pc 10–16.

Measurements (Table 1). Tube length 490–621 mm (n=8); outer width of top funnel opening 8.2–12.8 mm (n=7); bottom outer width of top funnel 7.4–11.1 mm (n=8); width of basal end of tube 0.8–2.3 mm (n=8). Body length 271–516 mm (n=8). Obturacular length 6.6–12.9 mm (n=8). Vestimental length 21.9–43.1 mm (n=8). Cuticular plaque length on vestimentum of paratype 78–88 μ m (mean 82 μ m, n=4), width 87–99 μ m (mean 94 μ m, n=4); length of plaques on trunk 49–85 μ m (mean

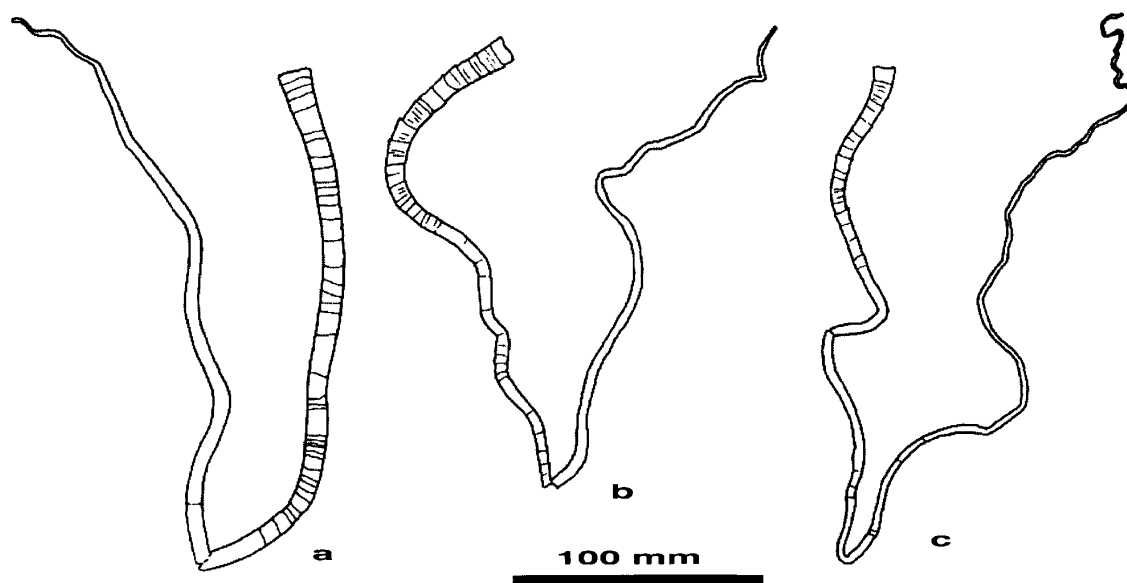


Fig. 1. Tubes of *Lamellibrachia juni* sp. nov., paratypes. a, NSMT-Pc 11; b, NSMT-Pc 12; c, NSMT-Pc 14.

73 μm , $n=5$), width on trunk 80–98 μm (mean 87 μm , $n=4$). Vestimental length/obturacular length ratio 2.7–3.9 ($n=8$). Vestimental length/obturacular width ratio 2.7–5.7 ($n=8$). Vestimental length/vestimental width ratio 3.1–6.0 ($n=8$).

Description. Tube wall thin enough to be cut easily by dissecting scissors, with obvious growth collars in anterior region (Fig. 1a–c); top funnel largest; funnel opening 1.1–1.3 times wider than stem; anterior end of stem up to 11.5 times wider than basal end of tube.

Anterior face of obturaculum of adult bare, lacking secreted structures (Fig. 2b), surrounded by up to 35 pairs of branchial lamellae (Fig. 2c, Table 1). Each lamella formed by single series of fused branchial filaments with pinnules. Branchial lamellae partially hidden by up to 3 pairs of peripheral lamellar sheaths without pinnules (Fig. 2a–c). Obturaculum flared distally, lenticular in transverse section.

Anterior margin of vestimentum forming a short collar extending around base of obturaculum. Paired genital ciliated grooves of middorsal vestimentum bounded by prominent parallel ridges in male, but inconspicuous and not bounded

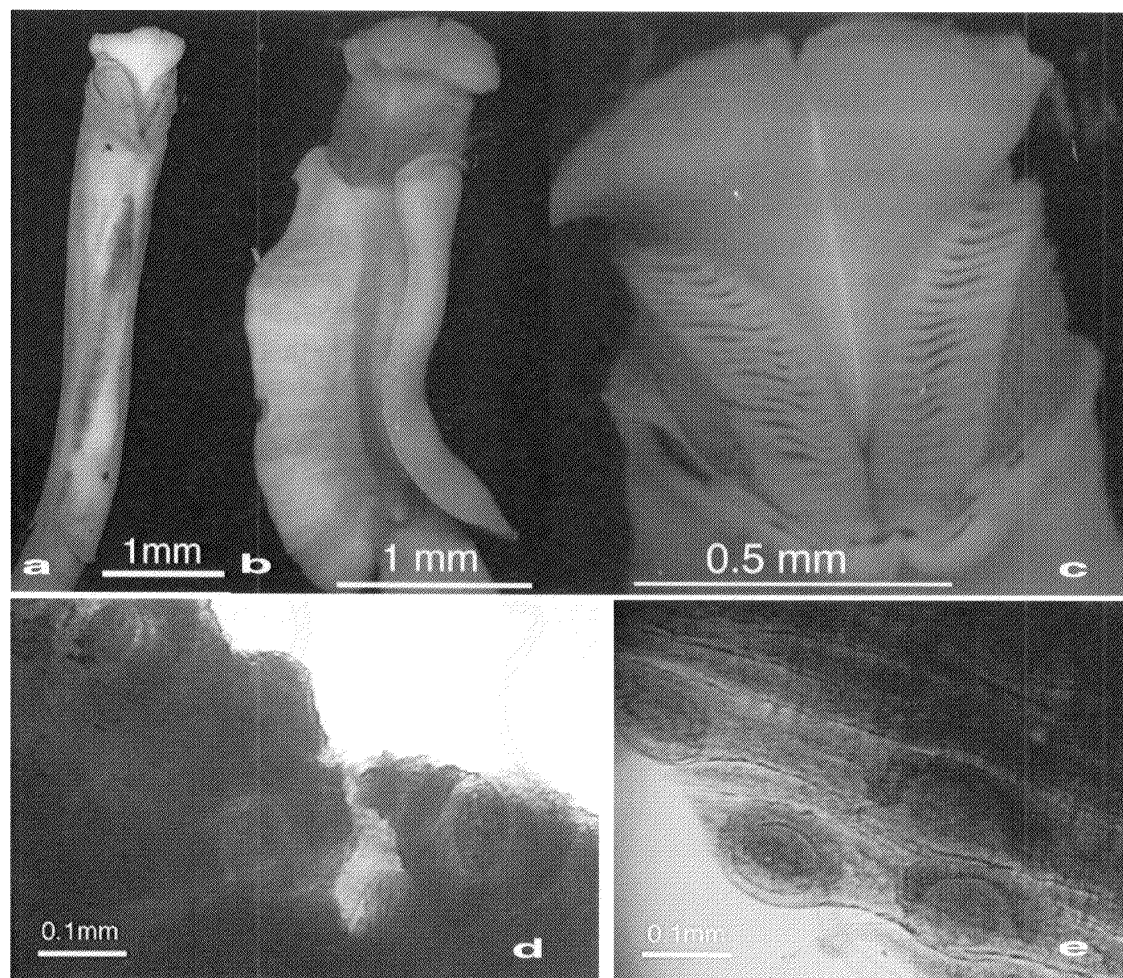


Fig. 2. *Lamellibrachia juni* sp. nov. a, Anterior end, ventral view; b, anterior end, dorsal view; c, anterior end, dorsal view; d, cuticular plaques of vestimentum; e, cuticular plaques of trunk. a, Paratype, NSMT-Pc 10; b–e, holotype, NSMT-Pc 9.

Table 1. Dimensions of type specimens in *Lamellibrachia juni* sp. nov.

| | Tube (mm) | | | Soft body (mm) | | | | | Branchiae (pairs) | | | | |
|----------------------|-----------|------------------|------|---------------------|--------|-------------|-------|-------------|-------------------|-----|---------------------------|--------------------|------------|
| | Length | Top funnel width | | Posterior end width | Length | Obturaculum | | Vestimentum | | Sex | Lamellar Branchial sheath | Branchial lamellae | State |
| | | Opening | Stem | | | Length | Width | Length | Width | | | | |
| | | | | | | | | | | | | | |
| Holotype, NSMT-Pc 9 | 503 | 12.1 | 8.7 | 0.8 | 271 | 7.8 | 8.3 | 25.0 | 8.1 | F | 3 | 27 | incomplete |
| Paratype, NSMT-Pc 10 | 555 | 11.9 | 10.8 | 0.9 | 411 | 9.4 | 7.6 | 36.4 | 7.5 | F | 2 | 35 | incomplete |
| Paratype, NSMT-Pc 11 | 515 | 12.8 | 11.1 | 1.7 | 373 | 12.9 | 8.0 | 43.1 | 7.6 | F | 2 | 32 | incomplete |
| Paratype, NSMT-Pc 12 | 490 | 11.1 | 10.1 | 1.1 | 360 | 10.7 | 7.4 | 42.0 | 7.0 | F | 2 | 25 | incomplete |
| Paratype, NSMT-Pc 13 | 490 | 10.7 | 8.2 | 2.3 | 406 | 7.0 | 7.0 | 26.0 | 6.9 | M | 3 | 28 | incomplete |
| Paratype, NSMT-Pc 14 | 580 | 8.2 | 7.4 | 1.2 | 516 | 9.5 | 5.2 | 27.9 | 5.8 | M | 2 | 23 | incomplete |
| Paratype, NSMT-Pc 15 | 504 | 8.7 | 7.8 | 1.1 | 439 | 6.6 | 8.1 | 21.9 | 6.5 | M | 2 | 22 | incomplete |
| Paratype, NSMT-Pc 16 | 621 | — | 8.5 | 1.1 | 334 | 12.8 | 8.1 | 35.5 | 8.0 | F | 3 | 27 | incomplete |

Table 2. Dimension of the species of the genus *Lamellibrachia*.

| | Tube (mm) | | Soft body (mm) | | Lamellar sheath (pairs) | VestL/ObtL | VesL/VesW | Cuticular plaque (μm) | | References |
|-------------------------|-----------|------------------|---------------------|---------------------|-------------------------|------------|-----------|-------------------------|---------|-----------------------------------|
| | Length | Top funnel width | Obtura-culum length | Vestimen-tum length | | | | Vestimen-tum (Diameter) | Trunk | |
| <i>L. barhami</i> | 1546 | 7.5-9.0 | 4.5-12.0 | 23-37 | 2-4 | 2.5-7.8 | 3-7 | 60-115 | 115-160 | Webb (1969) |
| <i>L. satsuma</i> | 317-1001 | 4.2-8.6 | 3.2-7.2 | 7.2-22.8 | 2-6 | 2.2-4.6 | 2.9-4.3 | 35-63 | 51-82 | Miura <i>et al.</i> (1997) |
| <i>L. luymesii</i> | 687 | 10 | 13 | 63 | 6* | 5 | 6.3 | 83-205 | — | Van der Land and Nørrevang (1975) |
| <i>L. victori</i> | 248 | 15 | 13 | 65 | 7 | 5 | 8 | — | — | Mañé-Garzón and Montero (1985) |
| <i>L. columna</i> | 820 | 14-20 | 15-42 | 60-120 | 8-16 | 2.2-4.5 | 6.5-13 | 65-90 | 70-120 | Southward (1991) |
| <i>L. juni</i> sp. nov. | 490-621 | 8.2-12.8 | 6.6-12.9 | 21.9-43.1 | 2-3 | 2.8-3.9 | 3.1-6.0 | 94-99 | 80-98 | present study |

* 4-8 in Gardiner *et al.* (2003).

by ridges in female (Fig. 2b). Posteroventral margin of vestimentum broadly incised (Fig. 2a), ventral surface with numerous small papillae topped by oval cuticular plaques with raised anterior margins (Fig. 2d).

Trunk very long, covered with numerous small papillae topped by cuticular plaques of almost same size as vestimental ones (Fig. 2e, Table 1).

Opisthosome not observed in incomplete types.

Remarks. *Lamellibrachia juni* sp. nov. is the only species in the genus with a flexible and thin-walled tube. All other species have very stiff and thick-walled tubes, e.g., 1 mm measured in *L. luymesii* Van der Land and Nørrevang, 1975 (*q.v.*). Furthermore, *L. juni* has up to three pairs of lamellar sheaths, which is the smallest number in the genus. The maximal number of lamellar sheath pairs is 16 in *L. columna* Southward, 1991, six in the holotype of *L. luymesii*, eight in the specimens of *L. luymesii* from the Gulf of Mexico reported by Gardiner *et al.* (2003), seven in *L. victori* Mañé-Garzón and Montero, 1985, six in *L. satsuma* Miura, Tsukahara and Hashimoto, 1997, and four in *L. barhami* Webb, 1969 (Table 2). The last species differs from the new species in the size of the cuticular plaques; *L. barhami* has bigger plaques on the trunk than on the vestimentum, while *L. juni* has similarly sized plaques in both areas.

Etymology. The species epithet is based on the first name of a Japanese pioneer in deep-sea research, Professor Jun Hashimoto of Nagasaki University, who found numerous hot vent and cold seep sites around Japan.

Genus *Oasisia* Jones, 1985

Diagnosis (emended). Vestimentiferans characterized by basal blood supply of branchiae and subtriangular or Y-shaped transverse section of obturaculum. Vestimentum with posterior fold entire. Obturaculum with dorsally grooved stalk; face with saucer-like projection or elongated flap. Distal branchial filaments with pinnules.

Type species. *Oasisia alvinae* Jones, 1985, by monotypy.

Remarks. The diagnosis of the genus is emended to accommodate the present new species.

Oasisia fujikurai sp. nov. (Figs 3, 4, Table 3)

Material examined. Holotype: Brothers Caldera, *Shinkai 6500* Dive 852, 27 October 2004, 34°51.671'S, 179°03.463'E, 1598 m, sex unknown, NSMT-Pc 17. Paratypes: same sampling data as holotype, 7 individuals including isolated opisthosome, sex unknown, NSMT-Pc 18–24. Non-types: same sampling data as holotype, 9 individuals, sex unknown, used only for measurement of tubes.

Measurements (Table 3). Length of selected tubes including those of paratypes 71–123 mm (n=14); opening outer width of top funnel 1.7–2.8 mm (n=14); bottom outer width of top funnel 1.4–2.2 mm (n=14); width of basal end 0.3–1.2 mm (n=14). Body length of almost complete paratypes 31–95 mm (mean 56.8 mm, n=5). Obturacular length 1.1–2.2 mm (n=6). Vestimental length 3.8–4.7 mm (n=6). Cuticu-

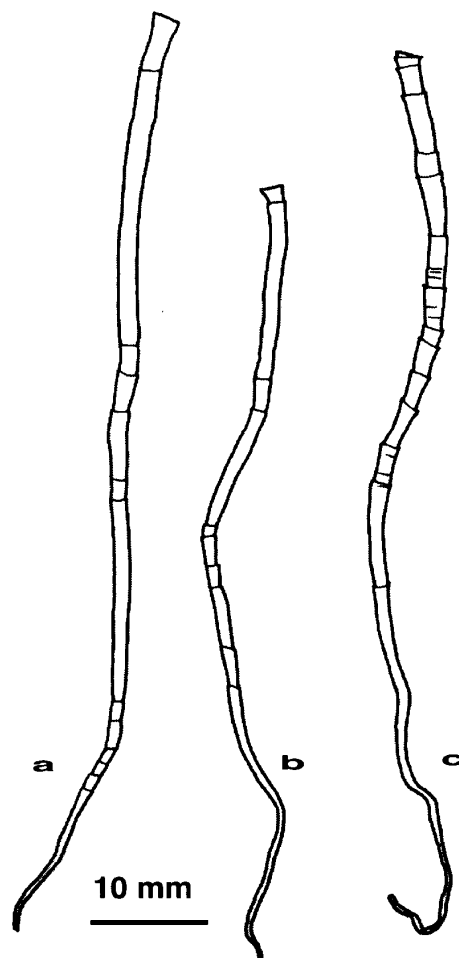


Fig. 3. Tubes of *Oasisia fujikurai* sp. nov., paratypes. a, NSMT-Pc 19; b, NSMT-Pc 22; c, NSMT-Pc 24.

lar plaque length on vestimentum of paratype 34–46 μm (mean 40 μm , $n=10$), width 43–58 μm (mean 51 μm , $n=10$); length of plaques on trunk 34–50 μm (mean 45 μm , $n=10$), width on trunk 57–68 μm (mean 62 μm , $n=10$). Vestimental length/obturator length ratio 2.7–3.9 ($n=8$). Vestimental length/obturator width ratio 1.8–4.1 ($n=6$). Vestimental length/vestimental width ratio 1.6–3.6 ($n=6$).

Description. Tube thin enough to be cut by dissecting scissors, with obvious growth collars in anterior half (Fig. 3a–c). Top funnel largest, funnel opening 1.1–1.5 times wider than stem, anterior stem up to 5.8 times wider than basal end.

Obturator flimsy, subtriangular in transverse section with broad dorsal groove and prominent ventral ridge. Anterior face of obturator in adults sometimes with elongated, flap-like projection, without rod-like structure or lamina (Fig. 4a, c), with 6 to 8 pairs of branchial lamellae and sometimes additional single ventral unpaired lamella (Table 3). Each lamella formed of single series of fused branchial filaments; most filaments pinnulate on their distal halves, but posterior lamellae with several non-pinnulate filaments; dorsal non-pinnulate filaments longer and thinner than pinnulate ones (Fig. 4b), ventral non-pinnulate filaments as thick as pinnulate ones. Lamellar sheaths absent.

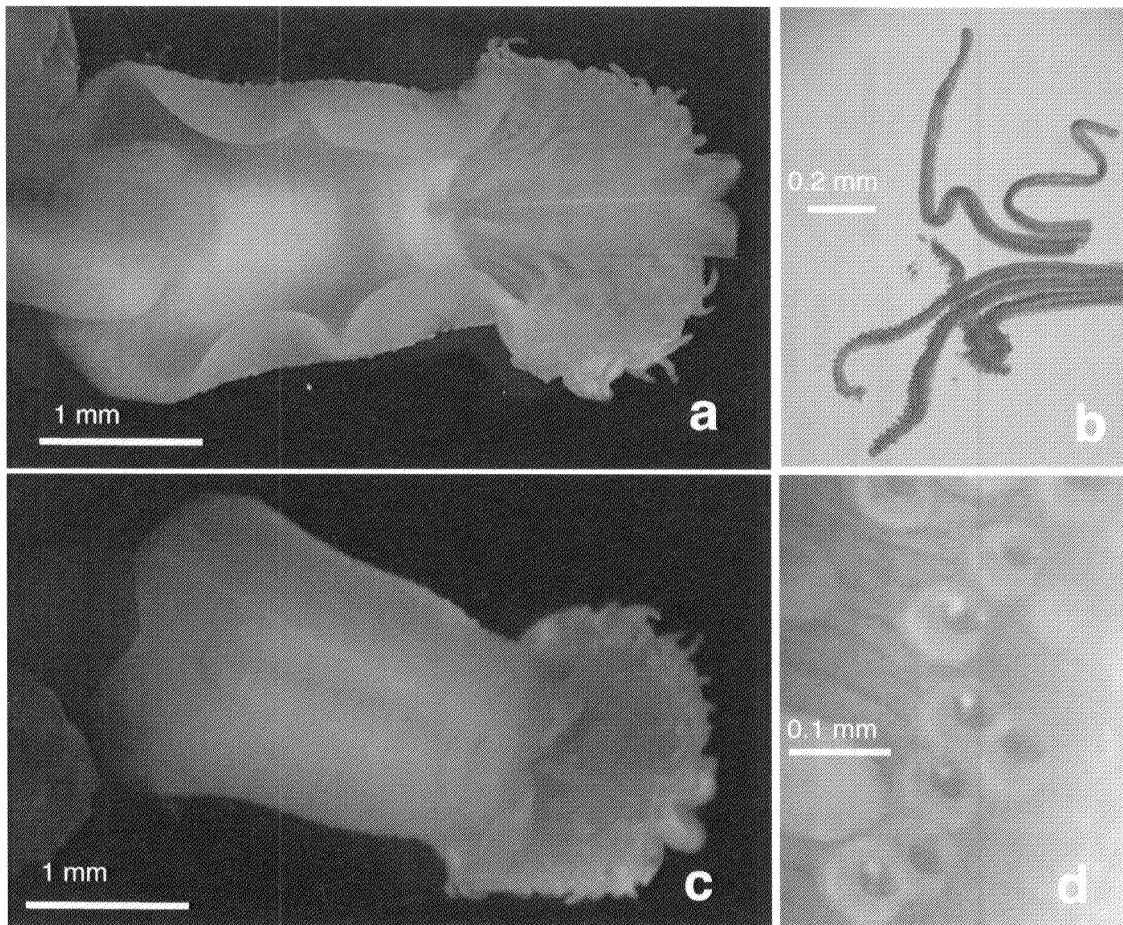


Fig. 4. *Oasisia fujikurai* sp. nov., holotype, NSMT-Pc 17. a, Anterior end, dorsal view; b, distal tips of branchial filaments; c, anterior end, ventral view; d, cuticular plaque of vestimentum.

Anterior margin of vestimentum forming a broad collar covering base of obturaculum. Posteroventral margin of vestimentum entire (Fig. 4c), ventral surface with numerous small papillae topped by oval cuticular plaques (Fig. 4d).

Trunk long, covered with numerous small papillae topped by cuticular plaques; trunk plaques larger than vestimental ones.

Isolated opisthosome (NSMT-Pc 24) preserved within type container with 9 anterior chaetigerous segments, 6 subsequent achaetigerous segments, and a terminal rounded segment. Chaetae arranged in single row along anterior margins of segments; most chaetae with 2 groups of denticles, anterior group including about 5 denticles in 2 rows, posterior group up to 12 denticles in 3 rows.

Remarks. The new species is classified in the emended genus *Oasisia*, which is characterized by the subtriangular shape in transverse section of the obturaculum, the stalk and face shape of the obturaculum, and the arrangement of the branchial pinnules. The new species differs from the type species by having up to eight pairs of branchial lamellae instead of up to 20 and by lacking a saucer-like medial obturacular structure.

Etymology. The species is named for Dr Katsunori Fujikura of JAMSTEC,

Table 3. Dimensions of type and non-type specimens in *Oasisia fujikurai* sp. nov.

| | Tube (mm) | | Soft body (mm) | | | | | | | | | | State of specimens |
|----------------------|--|---------|----------------|-----------|-------|-------------|--------|-------------|--------|--------------------|-------|------------------|---|
| | Top funnel width | | | Posterior | | Obturaculum | | Vestimentum | | Branchial lamellae | | | |
| | Length | Opening | Stem | end | width | Length | Length | Width | Length | Width | Pairs | Ventral unpaired | |
| | | | | | | | | | | | | | |
| Holotype, NSMT-Pc 17 | x | x | x | x | x | x | 2.05 | 0.67 | 3.76 | 2.40 | 8 | 1 | posterior part incomplete |
| Paratype, NSMT-Pc 18 | 71 | 2.06 | 1.63 | 0.35 | 0.35 | 31 | 1.36 | 0.85 | 3.90 | 1.26 | 6 | 2 | posterior part incomplete |
| Paratype, NSMT-Pc 19 | 95 | 2.47 | 2.07 | 0.70 | 0.70 | 95 | 1.88 | 1.77 | 4.68 | 1.47 | 6 | 1 | not pereserved well |
| Paratype, NSMT-Pc 20 | 87 | 1.79 | 1.44 | 0.25 | 0.25 | 66 | x | x | x | x | ? | ? | anterior and posterior parts incomplete |
| Paratype, NSMT-Pc 21 | 77 | 1.70 | 1.58 | 0.96 | 0.96 | 50 | 1.08 | 0.81 | 4.45 | 1.23 | 6 | 0 | anterior and posterior parts incomplete |
| Paratype, NSMT-Pc 22 | 78 | 2.03 | 1.60 | 0.82 | 0.82 | 42 | 1.38 | 0.63 | 3.87 | 1.24 | 6 | 0 | posterior part incomplete |
| Paratype, NSMT-Pc 23 | x | x | x | x | x | x | 2.21 | 0.93 | 3.89 | 2.18 | 8 | 1 | posterior part incomplete |
| Paratype, NSMT-Pc 24 | opisthosome specimen with 9 chaetigerous segments and 6 achaetigerous segments | | | | | | | | | | | | |
| Non-type specimen 1 | 75 | 1.95 | 1.37 | 0.67 | | | | | | | | | |
| Non-type specimen 2 | 92 | 2.52 | 1.78 | 0.51 | | | | | | | | | |
| Non-type specimen 3 | 71 | 2.13 | 1.39 | 0.33 | | | | | | | | | |
| Non-type specimen 4 | 82 | 2.57 | 1.71 | 0.65 | | | | | | | | | |
| Non-type specimen 5 | 73 | 1.96 | 1.60 | 0.56 | | | | | | | | | |
| Non-type specimen 6 | 75 | 2.01 | 1.87 | 1.19 | | | | | | | | | |
| Non-type specimen 7 | 91 | 2.47 | 1.91 | 0.50 | | | | | | | | | |
| Non-type specimen 8 | 88 | 2.67 | 2.16 | 0.56 | | | | | | | | | |
| Non-type specimen 9 | 123 | 2.81 | 1.99 | 0.58 | | | | | | | | | |

who provided the material examined in this study.

Results of Molecular Phylogenetic Analysis

Nucleotide sequences for 630 bp in the COI gene were determined for three individuals each of *Lamellibrachia juni* sp. nov. and *Oasisia fujikurai* sp. nov. Sequences from the three specimens of each respective species were identical. These sequences will be entered in the GSDB, DDBJ, EMBL, and NCBI nucleotide sequence databases under accession numbers AB242858 (*L. juni*) and AB242857 (*O. fujikurai*).

We analyzed the phylogenetic relationships among the two new species and other described or tentatively recognized species for which the nucleotide sequences of the upstream region of the COI gene have been reported by Black *et al.* (1997), Gardiner *et al.* (2001), Kojima *et al.* (2001, 2002, 2003), McMullin *et al.* (2003), and Andersen *et al.* (2004), on the basis of the nucleotide sequence of a region common to all studies (618 bp). For the MP method, the TV/TS ratio of 4:1, which corresponded to the observed ratio (3.666: 1), was used.

In the neighbor-joining (NJ) and maximum parsimony (MP) trees (Fig. 5), *Lamellibrachia juni* formed a monophyletic group with an as yet undescribed species, *Lamellibrachia* sp. L7, which has been collected only at the DESMOS site in the Manus Basin (Kojima *et al.* 2003). Their joint monophyly was supported by 100% bootstrap values for both methods.

Oasisia fujikurai formed a monophyletic group with *O. alvinae*, and this was also supported by high bootstrap values (>94%). *Ridgeia piscesae* Jones, 1985 formed a monophyletic clade with the *Oasisia* species on all MP trees, but this clade was supported by only a low bootstrap value (less than 50%). On the other hand, the monophyly of this clade was supported in the NJ analysis by a relatively high bootstrap value (70%). *Tevnia jerichonana* Jones, 1985 formed a monophyletic group with the *Oasisia-Ridgeia* clade on all MP trees and with *Riftia pachyptila* Jones, 1985 on the NJ tree, but these relationships were supported by low bootstrap values (<50%) and the phylogenetic relationships among *Tevnia*, *Riftia*, and the *Oasisia-Ridgeia* clade are at best inconclusive.

Discussion

Oasisia, *Tevnia*, and *Riftia* were erected each for a single species, while *Ridgeia* was erected for two species that were subsequently synonymized by Southward *et al.* (1995). These four genera formed a monophyletic group with the *Alaysia-Arcovestia* clade on all MP trees and on the NJ tree, based on molecular analysis (Fig. 5). *Riftia* is the only vestimentiferan genus characterized by an axial blood supply system to the branchiae (Table 4). *Tevnia* lacks obturacular saucers, as does *Riftia*, and thus differs from *Oasisia* and *Ridgeia* (Southward *et al.* 2002). The last two genera have been distinguished chiefly by the obturacular appendages and the number of rows of chaetal denticles (Jones 1985); however, with the synonymy of the two *Ridgeia* species (Southward *et al.* 1995) and the newly added morphological characters of the genus *Oasisia* in the present study, the dis-

Table 4. List of vestimentiferan genera and their character states.

| Genus | Branchiae | | | | Obturaculum | | | | Vestimentum | |
|--|--------------|-----------------|-----------------------|------------------------|-------------|-------------|-------------|-------------|----------------|-------------|
| | Blood supply | Lamellar sheath | Distal filaments with | Transverse section | Face | | Stalk | | Posterior fold | |
| | | | | | with rod/ | with | with dorsal | with dorsal | with dorsal | with dorsal |
| | axial (a) | present (+) | pinnules (+) | (s) (sub-) saucers (+) | lamina (+) | crust (+) | ridge (+) | groove (+) | present (+) | |
| | basal (b) | absent (-) | without (-) | triangular (t) | without (-) | without (-) | without (-) | without (-) | absent (-) | |
| <hr/> | | | | | | | | | | |
| <i>Lamellibrachia</i> Webb, 1969 | b | + | + | s | - | - | + | - | - | - |
| <hr/> | | | | | | | | | | |
| <i>Escarpia</i> Jones, 1985 | b | - | - | s | + | + | + | - | - | - |
| <i>Paraescarpia</i> Southward <i>et al.</i> , 2002 | b | - | + | s | + | + | + | - | - | - |
| <i>Seepiophila</i> Gardiner <i>et al.</i> , 2001 | b | - | + | s | - | + | + | - | - | - |
| <hr/> | | | | | | | | | | |
| <i>Oasisia</i> Jones, 1985 | b | - | + | t | + | + | - | + | + | + |
| <i>Ridgeia</i> Jones, 1985 | b | - | + | t | + | - | - | + | + | + |
| <i>Tevnia</i> Jones, 1985 | b | - | + | t | + | + | - | + | + | + |
| <i>Riftia</i> Jones, 1981 | a | - | + | t | - | - | - | + | + | + |
| <hr/> | | | | | | | | | | |
| <i>Arcovestia</i> Southward and Galkin, 1997 | b | - | + | t | - | - | - | + | + | + |
| <i>Alaysia</i> Southward, 1991 | b | + | + | t | - | - | - | + | + | + |

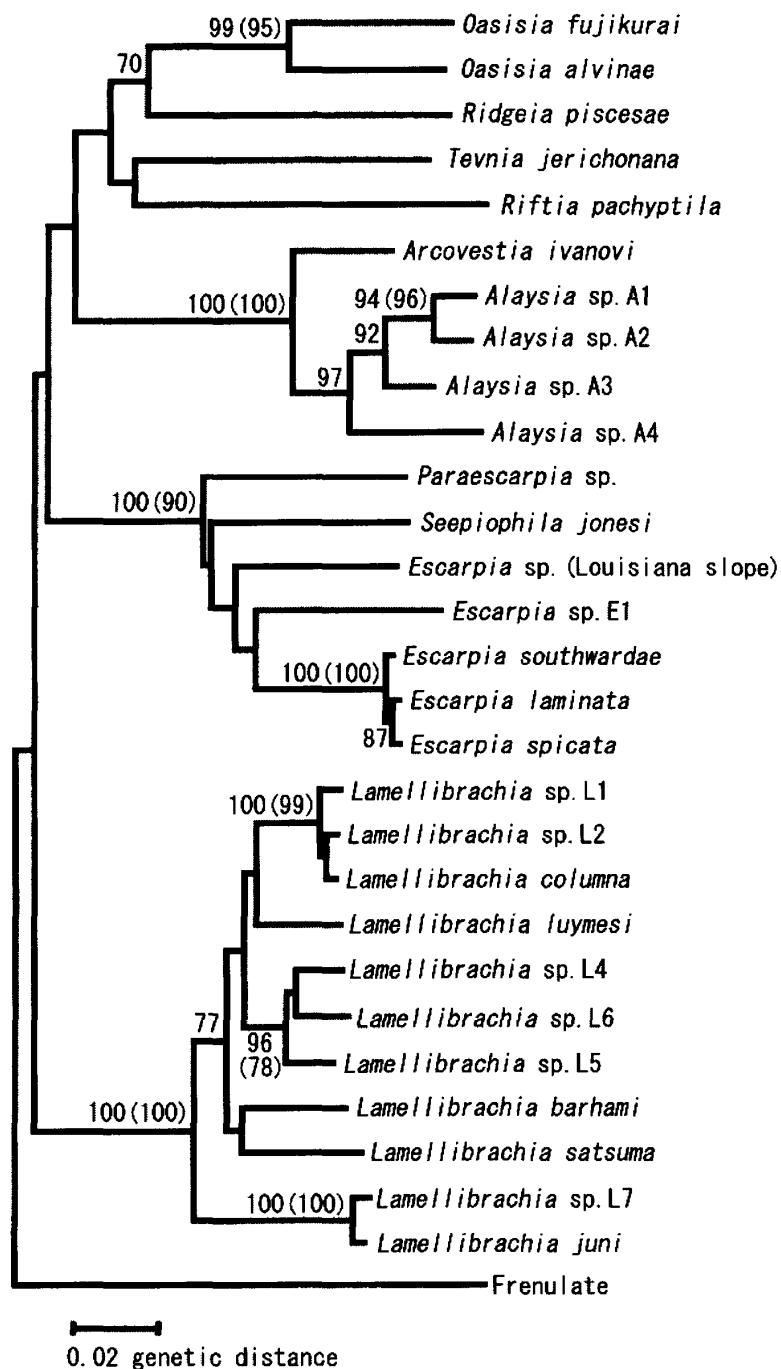


Fig. 5. Phylogenetic relationships among *Lamellibrachia juni* sp. nov., *Oasisia fujikurai* sp. nov., and other described or tentatively recognized species for which nucleotide sequences of the upstream region of the gene for cytochrome oxidase *c* subunit I were available, as analyzed by the neighbor-joining (NJ) method. An unidentified frenulate (tentatively identified as *Siboglinum* sp.) was used as the outgroup. Bootstrap probabilities are shown above or below branches of clades that are supported by bootstrap values of more than 70%. Bootstrap probabilities for the maximum-parsimony (MP) method are shown in parentheses when the values are greater than 70%.

tinctiveness of the obturacular appendages between the two genera becomes obscure and the morphology of the chaetae no longer distinguishes the two genera. We have classified *Oasisia fujikurai* in this genus by reason of the phylogenetic closeness demonstrated by the molecular analysis. Although the *Oasisia-Ridgeia* clade is clustered outside the other vestimentiferans with rather high bootstrap values (90% in Hurtado *et al.* 2002 and 70% in the present study's neighbor-joining analysis) and no significant morphological difference between the genera is present, *Oasisia* and *Ridgeia* are maintained as independent genera as long as *Ridgeia piscisae* is placed outside the *Oasisia* species clade.

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